

Abstract—Mayan cichlids (*Cichlasoma urophthalmus*) were collected monthly from March 1996 to October 1997 with hook-and-line gear at Taylor River, Florida, an area within the Crocodile Sanctuary of Everglades National Park, where human activities such as fishing are prohibited. Fish were aged by examining thin-sectioned otoliths, and past size-at-age information was generated by using back-calculation techniques. Marginal increment analysis showed that opaque growth zones were annuli deposited between January and May. The size of age-1 fish was estimated to be 33–66 mm standard length (mean=45.5 mm) and was supported by monthly length-frequency data of young-of-year fish collected with drop traps over a seven-year period. Mayan cichlids up to seven years old were observed. Male cichlids grew slower but achieved a larger size than females. Growth was asymptotic and was modeled by the von Bertalanffy growth equation $L_t = 263.6(1 - \exp[-0.166(t - 0.001)])$ for males ($r^2 = 0.82$, $n = 581$) and $L_t = 215.6(1 - \exp[-0.197(t - 0.058)])$ for females ($r^2 = 0.77$, $n = 639$). Separate estimates of total annual mortality were relatively consistent (0.44–0.60) and indicated moderate mortality at higher age classes, even in the absence of fishing mortality. Our data indicated that Mayan cichlids grow slower and live longer in Florida than previously reported from native Mexican habitats. Because the growth of Mayan cichlids in Florida periodically slowed and thus produced visible annuli, it may be possible to age introduced populations of other subtropical and tropical cichlids in a similar way.

Age, growth, and mortality of the Mayan cichlid (*Cichlasoma urophthalmus*) from the southeastern Everglades

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The Mayan cichlid, *Cichlasoma urophthalmus* (Günther), is native to the fresh and brackish waters of the Atlantic slope of Central America from Mexico to Nicaragua (Miller, 1966), where it is exploited commercially in artisanal fisheries and aquaculture (Martinez-Palacios and Ross, 1992). The first collections of the Mayan cichlid in the United States were made in 1983 from a freshwater habitat and a mangrove creek within Everglades National Park, Florida (Loftus, 1987). Although it remains unknown how or where Mayan cichlids first entered Florida waters, there is evidence that the discovery of this exotic fish was made shortly after their introduction (Loftus, 1987). Since their discovery, Mayan cichlids have expanded their range to include a variety of habitats from Naples (26°05'N, 81°48'W) to West Palm Beach (26°45'N, 80°04'W). The species remains abundant in the man-made freshwater canals and estuarine mangrove habitats of the region (Trexler et al., 2000).

The introduction of the Mayan cichlid into southern Florida has had both economic and ecological significance. This species supports a small sport fishery because it is edible, attractive, and

aggressively takes baits and artificial lures (Shafland, 1996). Anglers, however, have mixed feelings towards this fish because it readily takes artificial baits and fights hard on light tackle, and it can interfere with the pursuit of larger gamefishes, such as the common snook (*Centropomus undecimalis*). In some areas, the Mayan cichlid is the most common fish caught by recreational anglers and is targeted by subsistence anglers. There is concern, however that the interaction between Mayan cichlids and native fishes could alter the ecology of the Everglades and Florida Bay region. Although the role of Mayan cichlids as food for higher trophic-level fishes has not been quantified, they themselves are omnivorous and prey upon native fishes (Martinez-Palacios and Ross, 1988; Howard et al.¹).

Previous studies of the Mayan cichlid have focused almost entirely on its suitability for aquaculture in Mexico (e.g.

¹ Howard, K. S., W. F. Loftus, and J. C. Trexler. 1995. Seasonal dynamics of fishes in artificial culvert pools in the C-111 basin, Dade County, Florida. Final Rep. CA5280-2-9024, 34 p. and append. South Florida Research Center, Everglades National Park, Homestead, FL.

Martinez-Palacios and Ross, 1986; Flores-Nava et al., 1989; Ross and Beveridge, 1995) and on the potential for range expansion in the United States (e.g. Stauffer and Boltz, 1994). Few studies have addressed the life history of the Mayan cichlid, and only scant information exists on the age structure and growth rate of this species. From the seasonal length-frequency distributions for Celestun Lagoon, Mexico, Martinez-Palacios and Ross (1992) concluded that Mayan cichlids from 70 to 130 mm standard length had completed their first spring and were reproductively active, whereas individuals from 131 to 200 mm standard length had entered their second reproductive year. Observing no fish >200 mm, Martinez-Palacios and Ross (1992) concluded that the population of Mayan cichlids in the lagoon comprised fast-growing fish with one, or two (rarely), reproductive seasons in their lifetimes. Aging of Mayan cichlids using a validated method is needed to determine the accuracy of previously reported age and growth estimates and to compare the age structure between populations from Mexico and Florida. Here we provide a first account of the age, growth, and mortality of the Mayan cichlid from Florida waters.

Methods

Mayan cichlids were collected from the dwarf mangrove forests of southeastern Florida. This habitat is dominated by small (0.5–2.0 m tall) red mangrove trees (*Rhizophora mangle*) in an expansive, seasonally inundated wetland of typically shallow water (average maximum depth=30 cm). These mangroves increase in canopy width and height nearer to continuously inundated deeper creeks. The system is inundated mostly by fresh water during July–February but becomes more saline (10–35‰) during the dry season (March–June).

Cichlids <65 mm standard length (SL) were collected by using drop traps (Lorenz et al., 1997) to determine when Mayan cichlids first recruit. Drop-trap samples were collected every six weeks from August 1990 to September 1996 at Highway Creek, Joe Bay, and Taylor River (Fig. 1). Larger cichlids (>65 mm SL) were collected by using hook-and-line gear comparable to that used in other studies (Martinez-Palacios and Ross, 1992). Hook-and-line collections were conducted monthly from March 1996 to October 1997 in Taylor River, a major freshwater distributary of the Everglades emptying into northeastern Florida Bay. Each fishing effort continued until approximately 40 fish were obtained. Fish collected by both methods were measured (SL and total length [TL], mm), weighed to the nearest

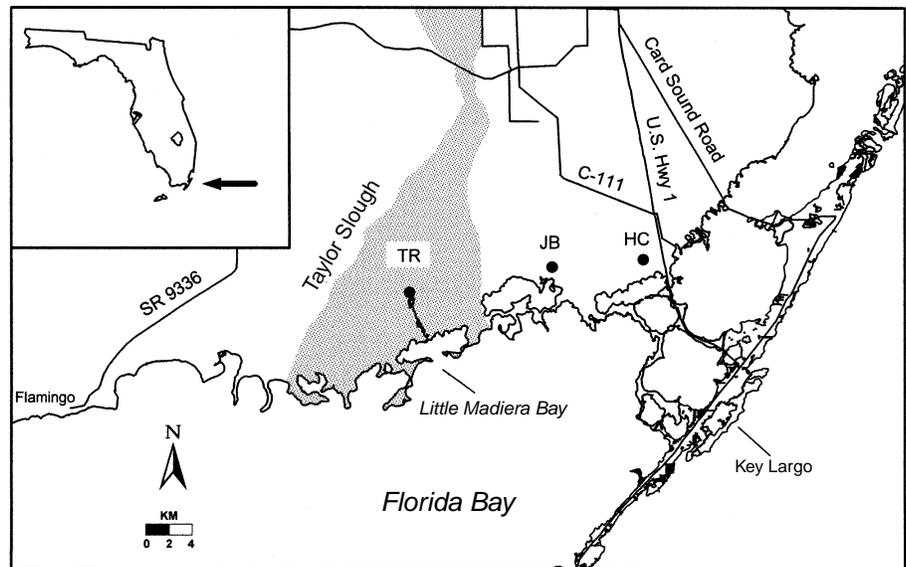


Figure 1

Map of southeastern Florida showing sampling locations (TR=Taylor River, JB=Joe Bay, HC=Highway Creek).

0.1 gram, and their sex was determined macroscopically when possible (Faunce and Lorenz, 2000). Fish captured during 1994–97 were used for age-and-growth analyses. All lengths reported hereafter are standard lengths.

Sagittal otoliths were removed, blotted dry, and stored in vials until they were sectioned. The left sagitta, unless broken, was used for age determination. Otoliths were sectioned by using a low-speed Beuhler Isomet saw with diamond blade. Three or four 0.5-mm thick transverse sections, one through the core, were cut and mounted on microscope slides with Histomount™ adhesive and allowed to dry. Sagittae from fish <100 mm were embedded in Spurr, a high-density plastic medium (Secor et al., 1992) and a 1–2 mm thick transverse section containing the otolith core was then cut. The sections were mounted on a microscope slide with Crystal Bond™ 509 adhesive, and polished with wet and dry sandpaper of grit sizes 220–2000 until growth rings were visible. A polishing cloth with 0.05-gamma alumina powder was used to remove scratches.

A standardized protocol for interpreting otolith growth zones was followed. When viewed with reflected light, the transverse sections of Mayan cichlid otoliths had two distinct regions: 1) an “inner region” extending from the core to the first visible opaque zone (ring), and 2) an “outer region” extending from the first visible opaque zone to the edge of the otolith (Fig. 2). The inner region was typically more opaque than the outer region and sometimes contained a visible growth zone or numerous check marks, or both. Unfortunately, these marks were difficult to interpret, inconsistent between sections from individual fish, and in many cases absent altogether. Consequently, we did not count any marks from the inner region in our age estimations. However, the translucent appearance of the outer region of the otolith made it possible to count distinct, separate, opaque rings when present. The number of rings

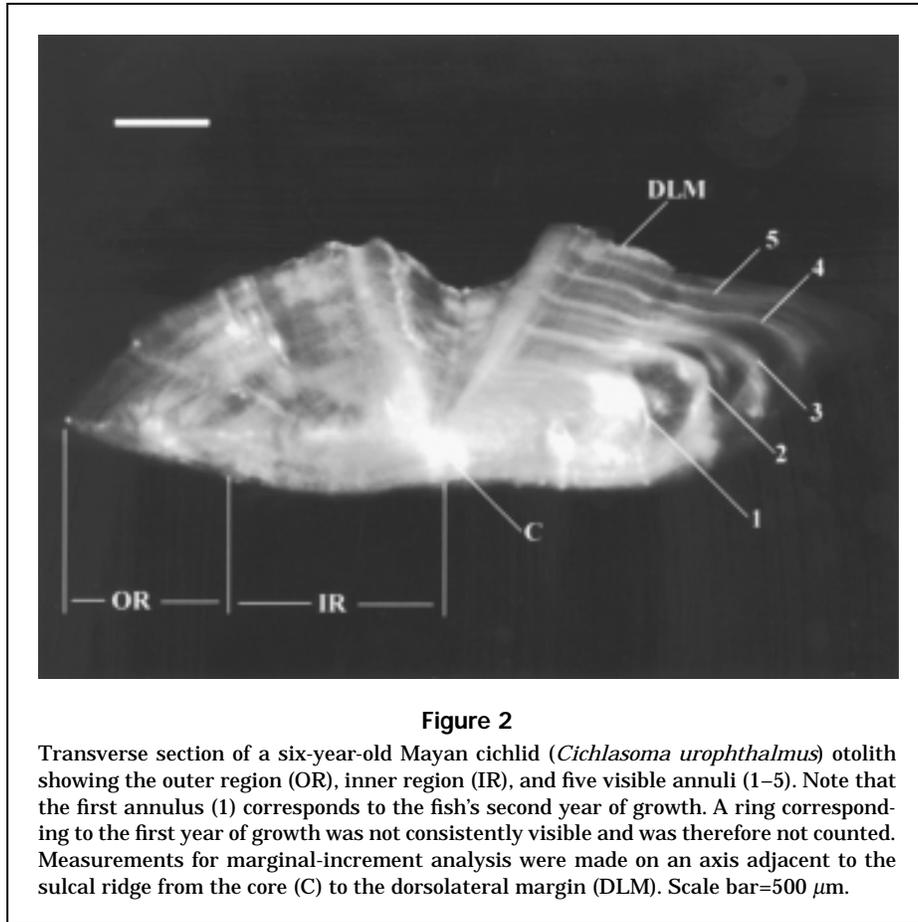


Figure 2

Transverse section of a six-year-old Mayan cichlid (*Cichlasoma urophthalmus*) otolith showing the outer region (OR), inner region (IR), and five visible annuli (1–5). Note that the first annulus (1) corresponds to the fish's second year of growth. A ring corresponding to the first year of growth was not consistently visible and was therefore not counted. Measurements for marginal-increment analysis were made on an axis adjacent to the sulcal ridge from the core (C) to the dorsolateral margin (DLM). Scale bar=500 μm .

on each otolith section was counted independently by two readers using compound microscopes, and the results were compared. If there was a discrepancy in the counts between readers, the section was re-examined. If a consensus could not be reached between the readers after the third reading, the otolith was excluded from the study.

Linear regression was used to determine the relationship of otolith radius to standard length and marginal-increment analysis was used to determine the periodicity of ring formation. Distance from the core to the proximal edge of each ring and to the dorsolateral margin of the otolith (otolith radius) was measured (Fig. 2). Measurements were made with a digital-image processing system along an axis adjacent to the sulcal ridge. The distance from the outermost ring to the dorso-lateral margin (i.e. marginal increment=MI) was plotted by month (marginal increment analysis). Because the majority of Mayan cichlids in Taylor River spawn during May and June (Faunce and Lorenz, 2000), and ring formation occurred during January–May, we assigned each fish a biologically realistic median hatching date of 1 June. Fish collected prior to 1 June that had not yet formed a new opaque ring (=high MI), and all fish collected after 1 June, were assigned a yearly age equal to their ring count. Fish collected before 1 June that had already formed a new opaque ring (i.e. an “early” ring) were assigned a yearly age of one less than their ring

count. To compare the timing of ring formation between age groups, marginal-increment analysis was performed on pooled ages 0–3 and 4–7 because our monthly sample sizes for individual age classes were insufficient for this analysis.

We used linear regression to determine the relationship between standard length and total length for all hook-and-line caught fish. The relationship between standard length and total weight was calculated separately for each sex with \log_{10} -transformed data. Analysis of covariance (ANCOVA) was used to test for significant differences between the slopes and intercepts of male and female length-weight relationships. Length-frequency distributions for males and females caught with hook-and-line were compared by using the Mann-Whitney rank sum t -test. Non-linear least squares procedures (SAS, 1989) were performed on final observed age-at-length data to estimate parameters for the von Bertalanffy growth equation

$$L_t = L_\infty(1 - \exp[-K(t - t_0)]),$$

where L_t = the standard length (mm);
 L_∞ = the asymptotic length;
 K = the Brody growth coefficient;
 t = the age (years); and
 t_0 = the age at zero length (von Bertalanffy, 1957).

To increase the number of observations used for fitting the growth model, we back-calculated past size-at-age information for each sexed fish using the Fraser-Lee method following Devries and Frie (1996);

$$L_i = [(L_c - a) / S_c] S_i + a,$$

where L_i = the back-calculated length of fish when the i^{th} increment was formed;

L_c = the length of fish at capture;

S_c = the otolith radius at capture; and

S_i = the otolith radius at the i^{th} increment.

The slope, $(L_c - a) / S_c$, was calculated for each fish as the slope of a line connecting two points: (S_c, L_c) and $(0, a)$. The y -intercept parameter a was determined from the relationship between otolith radius and standard length for all fish, and should approximate the fish length at which otolith radius equals zero (Devries and Frie, 1996). Because we could not accurately determine the sex of each fish <70 mm, fish whose sex could not be determined were included in the fitting of both male and female growth curves.

Catch curves were analyzed with two methods to determine annual mortality rates for Mayan cichlids. Survival rate (S) and its respective variance were estimated by using the empirical abundance data (Robson and Chapman, 1961) and the regression of the natural logarithm of year-class abundance (Ricker, 1975). The instantaneous rate of mortality (Z) was derived from the relationship $Z = -\ln(e^S)$. Total annual mortality (A) was computed as $A = 1 - S$. The age at full recruitment to the hook-and-line gear based on our catch curve was determined to be four years.

Results

The fragile nature of Mayan cichlid otoliths caused a high proportion (54%) to be lost during the cutting process. However, only five of the 391 successfully sectioned otoliths were discarded because a consensus between readers could not be reached. A newly formed opaque ring was generally observed in fish captured January–May, and the mean monthly marginal increment reached a single yearly minimum in June for all age classes examined (Fig. 3). These data indicate that the opaque rings observed were annuli.

The growth of young-of-year Mayan cichlids collected with drop traps could be followed by the progression of modal length from monthly length frequencies. Newly recruited fish were present in August (mode=10 mm) and grew to a size of 50 mm by June (Fig. 4). An early spawning event in 1993 (senior author, unpubl. data) produced a smaller-size (20 mm) cohort that was observed in June. Fish with one annulus were much larger (50–149 mm, mean=97 mm) than the size of age-1 fish suggested from our drop-trap data (June mode=50 mm). This information, combined with the presence of marks in the inner region

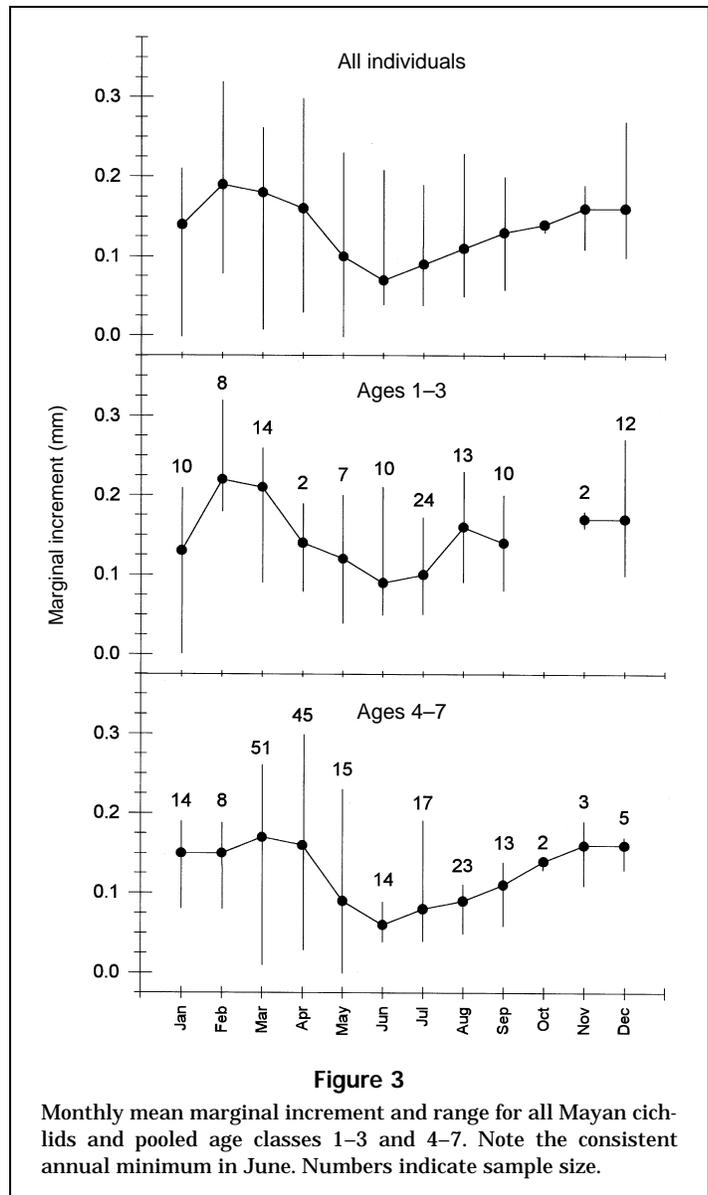
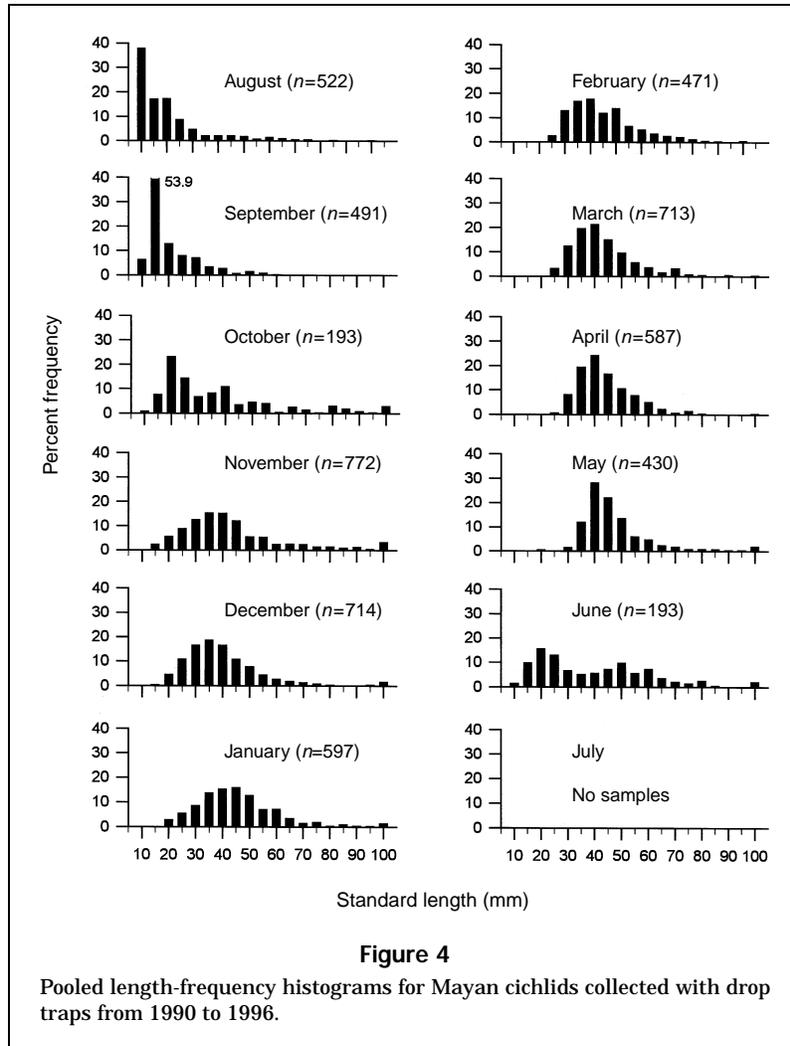


Figure 3
Monthly mean marginal increment and range for all Mayan cichlids and pooled age classes 1–3 and 4–7. Note the consistent annual minimum in June. Numbers indicate sample size.

of the otolith, led us to conclude that the first annulus in our age estimations was laid down between January and May of the fish's second year of growth, and we added a year to each individual's total age.

Length-length and length-weight relationships are given in Table 1. As required by the Fraser-Lee method for back-calculation of size-at-age information, otolith radius and standard length were closely related ($SL = 131.2 \times OR + 4.0247$, $n = 371$, $r^2 = 0.80$). Analysis of covariance did not detect differences between the slopes of length-weight relationships for males and females ($F_{1,839} = 0.15$, $P = 0.696$) but did reveal significant differences between the respective intercepts for males and females ($F_{1,839} = 4.10$, $P = 0.043$).

The length of Mayan cichlids at a given age was modeled by the von Bertalanffy growth equation (Fig. 5). Predicted lengths fitted well with the final adjusted observed



and back-calculated length-at-age data for males ($r^2=0.82$, $n=581$) and females ($r^2=0.77$, $n=639$). Our observed and back-calculated size of age-1 fish (mean \pm standard error = 45.5 ± 10.11 mm, range = 33–68 mm, $n=22$) corresponded well with the modal length of age-1 fish collected in drop-trap samples (50 mm). Differences in the parameter estimates for the von Bertalanffy growth equation were observed for each sex. Males were larger than females for all ages (Table 2). Although males exhibited a slower growth rate (K) and larger maximum attainable size (L_∞) than females, the von Bertalanffy growth model parameters were not significantly different between sexes (95% CI, Table 3). Male and female Mayan cichlids up to seven years old were observed.

The size of fish examined ranged from 21 to 210 mm (median = 127 mm, interquartile range = 98 mm, $n=1046$). Males ranged from 69 to 210 mm (median = 137 mm, interquartile range = 119 mm, $n=400$), and females ranged from 58 to 190 mm (median = 132 mm, interquartile range = 115 mm, $n=449$) (Fig. 6). The length-frequency distribution for males was significantly larger than that for females ($P < 0.001$). The overall ratio of males to females was 1:1.1.

Age-frequency distributions of Mayan cichlids collected by hook-and-line gear suggest that these fish are fully recruited to the fishery at age four (Fig. 7). The majority of males (85.1%) and females (81.5%) were 3–5 years old, and there was a significant difference (Mann-Whitney rank sum t -test, $P < 0.001$) in the age-frequency distribution of males (median = 3.67 years, interquartile range = 2.12) and females (median = 4.78 years, interquartile range = 3.86). Total instantaneous mortality (Z), annual survival (S), and annual mortality (A), based on the regression of our catch-curve data, were estimated at 0.57, 0.56, and 0.44, respectively ($r^2=0.91$, $n=3$). Robson and Chapman (1961) estimates were $Z=0.91$, $S=0.40 (\pm 0.035)$, and $A=0.60$.

Discussion

Transverse otolith sections can be used to precisely age Mayan cichlids from Florida waters. There was a high congruence (98.7%) between the age estimations of each reader. Annuli corresponding to years 2–7 were clearly

Table 1

Length-length, length-weight, and otolith-radius–standard-length regressions for the Mayan cichlid, *Cichlasoma urophthalmus*, from Taylor Slough, Florida. Regressions are in the form $Y = a + bX$. TL = total length (mm); SL = standard length (mm); WT = total weight (g); OR = otolith radius (mm); range = sample standard length range in regressions. Values in parentheses are standard errors.

Y	a	b	X	n	Range (mm)	r^2
Sexes combined						
TL	0.6220 (0.2875)	1.3067 (0.0022)	SL	961	40–210	0.997
SL	-0.1281 (0.2202)	0.7631 (0.0013)	TL	961	40–210	0.997
SL	4.0247 (3.2740)	131.2092 (3.4214)	OR	371	33–210	0.800
$\log_{10} WT$	-4.2490 (0.0257)	2.9314 (0.0122)	$\log_{10} SL$	847	58–210	0.986
Males						
$\log_{10} WT$	-9.7958 (0.0874)	2.9329 (0.0178)	$\log_{10} SL$	395	84–210	0.986
Females						
$\log_{10} WT$	-9.7387 (0.0856)	2.9232 (0.0176)	$\log_{10} SL$	444	89–182	0.984

visible on the otoliths. The annulus corresponding to the first year's growth was not consistently clear to the readers, which has been observed in thin-sectioned otoliths of other fish species in Florida. Murphy and Taylor (1994) found that the first annulus was visible only in certain individuals of spotted seatrout, *Cynoscion nebulosus*. Similarly, Murphy and Taylor (1990) found that the annulus corresponding to the first winter or spring was absent in red drum, *Sciaenops ocellatus*. Direct validation of marked otoliths is needed to confirm the presence and location of the first annulus on the otolith of Mayan cichlids.

We observed differences in the growth patterns of males and females that are likely linked to reproduction. Males were larger than females and did not appreciably slow their growth with age. The nearly linear growth of males resulted in a theoretical maximum size (L_{∞}) of 263.6 mm, well above the ~200 mm commonly observed for this species (Loftus, 1987; Martinez-Palacios and Ross, 1992; present study). Larger males are common in riverine and lagoonal populations of tilapias (Cichlidae) and may have a selective advantage during the reproductive season if they can defend a spawning pit or brood against potential predators (Lowe-McConnell, 1982). Because sperm production requires less energy than egg production (Jalabert and Zohar, 1982), the slowed growth observed in females compared with that for males is likely due to differences in energy budgets during the reproductive season.

No significant differences were found by ANCOVA in the slopes of sex-specific length-weight relationships, but there were significant differences in the intercepts of those lines. Because the actual difference between the y -intercepts (weight) of each length-weight relationship was <0.001g, we attribute no biological meaning to the statis-

Table 2

Average predicted and observed standard lengths (mm) for male and female Mayan cichlids.

Age (yr)	Predicted	Average observed	Standard error	n
Males				
1	40.3	45.5	2.2	22
2	74.4	74.3	1.12	148
3	103.4	102.0	1.24	152
4	127.9	127.1	1.36	139
5	148.7	147.8	1.66	88
6	166.3	173.0	2.56	28
7	181.1	206	1.32	4
Females				
1	36.4	45.5	2.16	22
2	68.4	70.6	1.05	156
3	94.7	96.8	1.31	160
4	116.3	119.8	1.4	151
5	134.0	137.0	1.59	102
6	148.6	148.1	1.94	45
7	160.6	151.0	3.22	3

tical difference and consider the length-weight relationships for both sexes to be equal.

Mayan cichlids in Florida were much smaller at a given age than those reported by Martinez-Palacios and Ross (1992) in Mexico. One-year-olds were 33–66 mm in Florida vs. 70–130 mm in Mexico, and age-2 fish were 44–130 mm

Table 3

Parameter estimates for the von Bertalanffy growth model (1957) for Mayan cichlids and associated standard error (SE) and confidence intervals (CI).

Sex	L_{∞} (mm)	K	t_0 (yr)	n	r^2
Males	263.66	0.165	0.001	581	0.82
SE	25.15	0.027	0.124		
95% CI	49.28	0.053	0.243		
95% CI range	214.34–312.95	0.112–0.218	0.242–0.244		
Females	215.63	0.197	-0.058	639	0.77
SE	17.33	0.031	0.142		
95% CI	33.96	0.061	0.278		
95% CI range	181.67–249.59	0.136–0.258	-0.336–0.220		

in Florida and 131–200 mm in Mexico. We found a maximum age of seven years, whereas two years was suggested by Martinez-Palacios and Ross (1992). We offer three explanations for these observed differences in the length-at-age data. First, exploitation rates may differ between

study areas. Fish in our study came from the Crocodile Sanctuary within Everglades National Park and had not been exposed to fishing mortality. Fishing for Mayan cichlids occurs outside of our study area, and heavy exploitation can select for faster-growing fish with a shorter life-span (Ricker, 1975). Martinez-Palacios and Ross

(1992) suggested that their population was overfished. Second, differences in temperature impact fish growth. Colder winter temperatures in Florida were sufficient to form seasonal marks in the otoliths of Mayan cichlids and may have caused slower growth than in Mexican populations. Third, the seasonal length frequencies of Martinez-Palacios and Ross (1992) were insufficient to accurately identify older year classes. Because growth slows with age, the length-frequency of cohorts corresponding to older age classes can overlap significantly, resulting in erroneously lower age estimates. Future efforts to age Mayan cichlids in Mexico should include thin-sectioned otoliths to evaluate the findings of Martinez-Palacios and Ross (1992).

Although the Mayan cichlid has proliferated for over a decade in the natural and man-made habitats surrounding the Everglades, studies are only recently becoming available (e.g. Trexler et al., 2000). More introduced fish species are found in Florida than in any other state in the United States, and 13 of the 18 species with established populations are cichlids (Shafland, 1996). The impact of exotic species on native Florida fishes has been debated: Shafland (1996) proposed no demonstrable effect on native fishes, whereas Courtenay (1997) argued that lack of available data precludes a determination. Trexler et al. (2000) provided empirical data that support Shafland (1996), concluding that although exotics have been credited with native species extinctions in other ecosystems, native Florida fishes are not specialized or restricted to certain habitats and thus are able to cope with the invasion of exotics. Finding no drastic changes in the native ichthyofauna does not necessarily mean that exotic species do not affect indigenous fishes. Exotic species can introduce

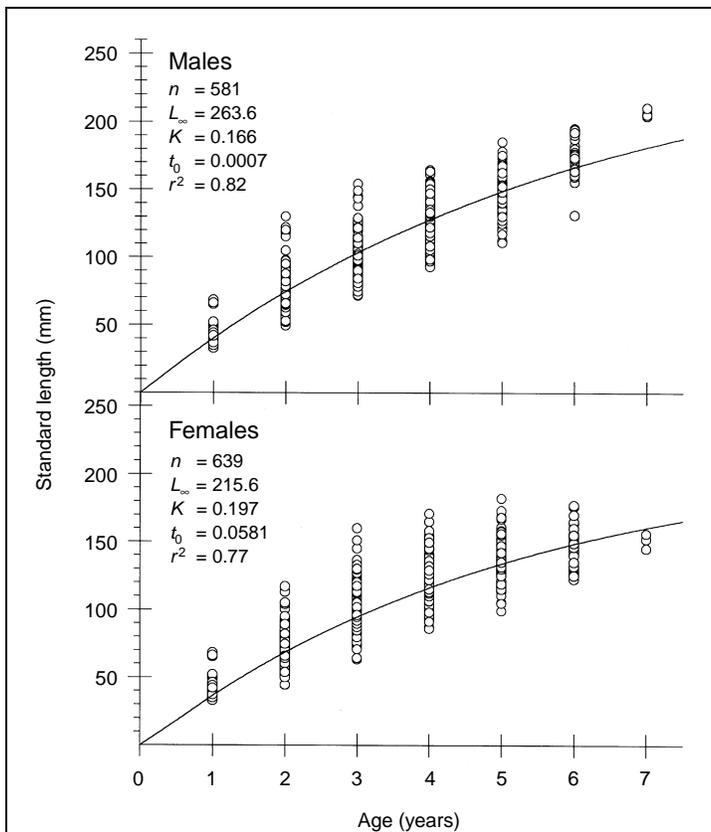


Figure 5

Observed and predicted lengths at age for male and female Mayan cichlids from the von Bertalanffy growth model. n —observed and back-calculated size-at-age information from 148 males and 157 females.

numerous stresses not easily quantified, e.g. nest predation, direct predation, and competition for space (Trexler et al., 2000; senior author, unpubl. data). These stresses may affect the population dynamics of native fishes by altering their growth rate, increasing mortality, or decreasing reproductive success. During 1990–99, the Mayan cichlid population underwent a cyclical “boom and bust” pattern of yearly abundance typical of invasive species (Trexler et al., 2000). Why these patterns occur requires a better understanding of the parameters of reproduction, growth, and mortality that drive the population dynamics of this species. The presence of the Mayan cichlid in the Everglades and Florida Bay estuary warrants further research and monitoring efforts in the region to firmly understand the life history of exotics, native fishes, and their role in the ecosystem.

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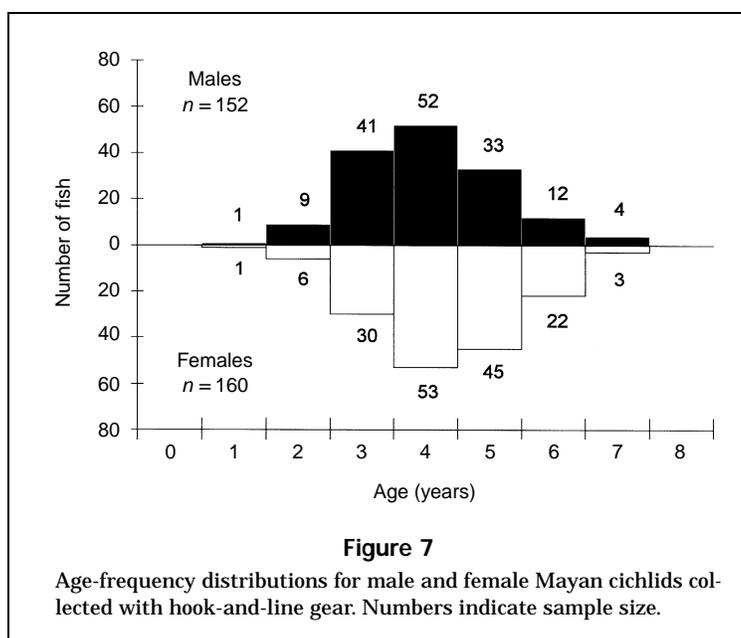
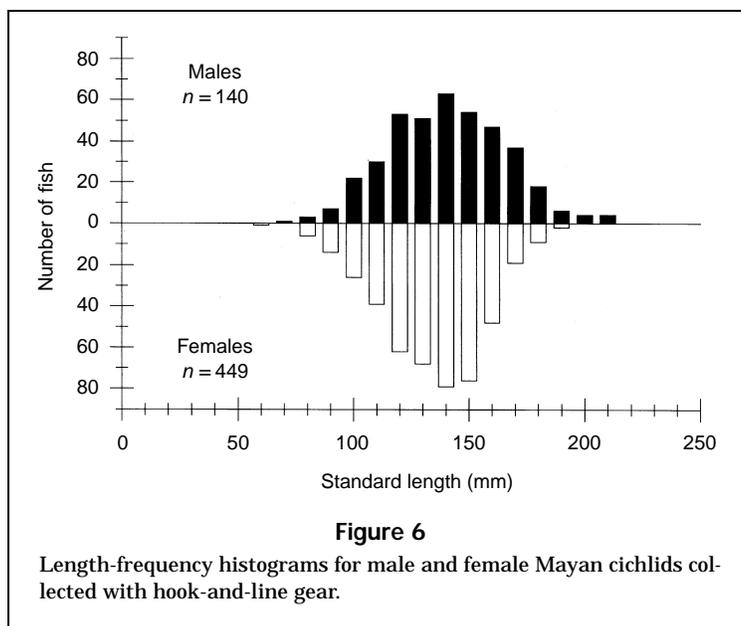
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